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# Swimming and search behaviour in clownfish, *Amphiprion perideraion*, larvae

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**Abstract.** The swimming behaviour and search patterns of pink clownfish larvae, *Amphiprion perideraion*, were examined using a novel filming apparatus that permits three-dimensional tracking of free swimming zooplankters. Analysis of the resulting search paths included swimming speed and average turning angle, as well as a new approach to the study of search dynamics, fractal analysis. *Amphiprion perideraion* larvae display a clear shift in behaviour at the onset of feeding, with a drop in overall complexity of their swimming paths and an increase in their swimming speed. Similar to other foraging animals, clownfish larvae display at least two search modes after the onset of feeding: a highly linear ranging mode used to locate patches of food and a highly complex, convoluted searching mode used to exploit those patches once they are located. Conventional analysis did not adequately discriminate between foraging modes, creating the need for fractal analysis. Unlike other foraging animals, clownfish larvae increase swimming speed when they encounter patches of high food abundance. This response is proposed to be the result of hydrodynamic constraints imposed upon the fish because of their relatively small size.

Research on the search behaviour of terrestrial organisms and adult fish has made great strides in quantitatively describing and modelling search paths (e.g. Wehner & Srinivasan 1981; Harkness & Maroudas 1985; O'Brien et al. 1989). Zooplankton, including fish larvae, operate under very different conditions to these organisms. Because zooplankton are small and travel at high rates of speed relative to body size, researchers have been unable adequately to observe their movement in three dimensions. The search behaviour of zooplankton has, therefore, not been adequately researched.

Recent technological advances have made it possible to track small free-swimming zooplankters, both invertebrate and vertebrate. A filming apparatus termed the CritterSpy, developed in this laboratory, enables researchers to track and observe small aquatic organisms. A great advantage of this apparatus is its ability to record accurately, at a relatively high rate, an animal's position within the filming vessel. The video images of the system are sufficiently magnified to allow observation of the details of feeding and swimming behaviour. In addition, the position data produced by the CritterSpy permit the use of novel forms of analysis such as the calculation of the fractal dimension of swimming paths.

This study describes in detail the search patterns and swimming behaviour of clownfish larvae, *Amphiprion perideraion*. Our aim in this study was to determine accurately the responses of fish larvae to changes in their environment, such as an increase in prey abundance. Since fish larvae in the sea may depend on high-density patches of food (Jenkins 1988), we predicted that *A. perideraion* larvae, like other fish larvae, would respond to higher food abundance with a non-random change in its search behaviour.

Many foraging organisms generally display at least two foraging modes while searching for food to efficiently exploit patchy food resources. In the first mode, a ranging type of behaviour (Jander 1975; Bell 1985) is used to locate specific patches of high food abundance. This behaviour pattern consists of an animal travelling by alternating erratic turns with straight stretches. The second mode is used when a patch of food is encountered. A foraging animal initiates a local search (Jander 1975) or an area-restricted search (Krebs 1973) to exploit

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that patch. During a local search an animal travels in highly convoluted patterns of 'tangled, looping, intersecting paths without straight sections' (Jander 1975). Additionally, local search often involves a reduction in the speed of movement. By travelling in complex looping patterns and slowing the rate of movement, an animal tends to maximize the time it spends in an area of perceived high prey abundance (Bell 1985).

Some sort of local search, or non-random response to prey encounter, is used by a wide variety of animals, including planaria (Mason 1975), ants (Schmid-Hempel 1984; Harkness & Maroudas 1985; Traniello et al. 1991), other arthropods (Bell 1985), copepods (Williamson 1981; Cowles & Strickler 1983), birds (Smith 1974; Pienkowski 1983), adult fish (Beukema 1968; Marschall et al. 1989), and fish larvae (Rosenthal & Hempel 1970; Wyatt 1972; Hunter & Thomas 1974; Munk & Kiorboe 1985). The wide usage of at least some sort of local search is indicative of its efficiency in exploiting a patchy habitat and its relevance to researchers in other taxa.

Because zooplankters are relatively small, the hydrodynamic conditions under which they operate differ from those of larger aquatic organisms (see Strickler 1984). The effect of viscosity is much greater for small aquatic organisms, such as fish larvae, than for either large aquatic or terrestrial organisms. We predicted that the hydrodynamic constraints of the viscous environment would affect the mobility of clownfish larvae and, therefore, alter their response to changes in prey density.

In addition to our analysis of the observed swimming paths of fish larvae, we also attempted to model these paths of swimming clownfish larvae. By generating a model, programmed with certain path characteristics, different paths were randomly created which ranged from nearly linear to highly convoluted. Therefore, encounter rate experienced by a hypothetical fish larvae for different path types, at several food densities, could be evaluated to allow a comparison of observed fish larvae behaviour with path shapes that maximize prey encounter rate.

## METHODS

We obtained pink clownfish larvae, *A. perideraion*, from the New England Aquarium. We collected them immediately after hatching and quickly transported them to the Biology Research Building at Boston University, where the larvae were reared and all experiments were carried out. We used two consecutive batches of full-sibling larvae from the same breeding pair in this experiment. At hatching, the larvae are relatively small (approximately 4 mm), and do not begin feeding until 2–3 days later.

We reared the larvae in 38-litre aquaria contained within an environmental chamber. The temperature was maintained at 24°C during rearing and experimentation, and bright fluorescent lighting was supplied on a 12:12 h light:dark cycle. There was no aeration or other mixing of the water. For the first 5 days the fish were fed rotifers, *Brachionus* sp., at a density of 1000 rotifers per litre. After 5 days, we fed them a mixed diet of rotifers and *Artemia* nauplii.

### Filming of Fish Larvae

Experimental design entailed tracking free-swimming clownfish larvae in two densities of rotifers: low (20–30/litre) and high (1000/litre). We filmed the first batch under the high-density condition on day 1 (the day of hatching), and under low- and high-density conditions on days 2, 3 and 5. We filmed the second batch under low- and high-density conditions on days 1 and 3, and under the low-density condition on day 7. The experimental food densities were chosen because previous research has found clear differences in larval behaviour in relation to food densities that were very low and very high ($<50$ prey/litre and $>360$ prey/litre, respectively; e.g. Munk & Kiorboe 1985). A visual survey during experiments indicated that the rotifers were not forming micro-patches within the filming vessel.

We carried out video-recording of clownfish larvae swimming patterns using the CritterSpy filming apparatus. This apparatus consists of two video cameras mounted at right angles to each other, providing front and side views of a filming vessel with an image magnification of 15× (Strickler 1985). The position of a fish larva in all three dimensions within the filming vessel was derived from the two views. Because a dark-field modified-Schlieren optical system was used (Strickler 1985), larvae were visible in profile as dark shapes with bright, white borders. Rotifers were visible as small oval shapes; algae, dust and other particles greater than 20 μm in size were clearly visible as bright points of light. The CritterSpy video

equipment includes: electronically shuttered Pulnix TM-845 video cameras, Panasonic NV-8500 VCRs and Sony Triniton 13 inch and Panasonic WV-5470 19 inch video monitors. The electronic shutter speed was 1/8000 s, providing clear images. The filming vessel was lit from above with strong white light from a fibre optics lamp. The Schlieren optical pathway was lit with a helium-neon 1-mW laser emitting red light at a wavelength of 632 nm. Most of the fish swam and fed actively under the filming conditions; fish that behaved abnormally by spending inordinate amounts of time on the bottom or surface were not included in this study.

We tracked free-swimming animals by viewing them on the two video monitors. When animals moved away from the centre of a camera view, the camera and/or vessel was repositioned to return the fish to the centre of the video monitor. This repositioning was directed manually by two researchers, using a three-dimensional MicroSpeed FastTRAP trackball and computer keyboard connected to an AST Premium/386 computer. We used software written in the C computer language to control the CritterSpy. The cameras were mounted on a platform and could be moved in the horizontal dimensions ($X$ and $Y$), while the filming vessel and the water containing the animals and prey were moved in the vertical dimension ($Z$) to avoid 'sloshing', secondary water currents and turbulent water flow. The filming vessel was also isolated from any vibrations of the horizontal motors. The computer that directed the movement of the linear positioning motors also logged the position of the horizontal motors at each point in time at a rate of 10–15 Hz and a minimum spatial increment of approximately 50 µm.

On each filming day, 5 litres of filtered sea water was placed in the filming vessel. We added rotifers to reach the low prey density condition of 20–30/litre, and then placed 8–10 larvae in the CritterSpy filming apparatus. The CritterSpy has a recirculating water bath that maintained the filming vessel temperature at 24–25°C. After a 30-min period of acclimation, clownfish larvae were filmed for a 1-h period. After the first filming period, we increased the concentration of rotifers to 1000/litre by gently mixing in 5–10 ml of water containing a sufficient number of rotifers. After another 30-min acclimation period, we filmed the fish for an additional 1-h period.

During a filming period, the operators tracked one fish for as long as possible. This usually lasted 1–2 min, but could be as long as 5–6 min. When a fish was lost from view, or swam within a body length of a wall, the bottom, or the surface, the operators would pick another actively swimming fish within the vessel and attempt to follow it.

Each filming period resulted in the following data: a large computer database containing the temporal position data ($X_i$, $Y_i$, $Z_i$, $t_i$) of all fish filmed, a videotape recording of the $X$–$Z$ view during filming and a second videotape of the $Y$–$Z$ view. The database and the video recordings were linked by visual frame numbers on the videotapes, which corresponded to the time that each position was recorded in the computer file.

### Analysis of Swimming Paths

Segments of the video-recording in which a fish was centred in each camera view (i.e. within half a body length from the centre of video monitor) for at least 30 s were considered valid swimming paths. If the image of a swimming larva remained centred in the video monitor, then it was tracked accurately. Also, a 30-s path was of sufficient duration to allow fractal analysis (see below). The position data of each segment were obtained from the computer database.

The fish were identified individually by their total length as measured on the video screen. On day 1, the swimming paths of a total of 12 fish were analysed. We analysed seven fish on each of days 2 and 3, five fish on day 5 and three fish on day 7. Individual fish were filmed on one day only. For each fish, between three and five swimming paths were studied at each food density, where possible; paths averaged 50 s in duration. The tracks were analysed for several different characteristics: net movement, gross movement, net to gross displacement ratio (NGDR, see below), swimming speed, average turning angle, and fractal dimension ($D_f$).

The ratio of net movement (the distance from the first point to the last point in the database of a single swimming path) to gross movement (the sum of distance moved between each consecutive position point) is termed NGDR (Wilson & Greaves 1979). We used NGDR (range = 0–1) as an indication of the turning rate of a path of a swimming animal. Highly linear movement corresponds to a high NGDR value, while highly convoluted, looping movement corresponds to a low NGDR value. Swimming speed is the result of dividing gross movement by the length of time of the path.

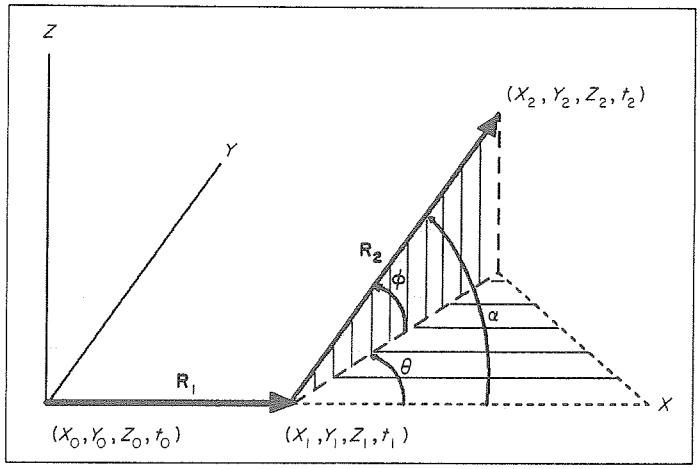


**Figure 1.** Definitions of turning angles used in the analysis of swimming paths of *A. perideraion* larvae. α is the angle in three-dimensional space between the vectors $\mathbf{R}_1$ and $\mathbf{R}_2$. θ is the horizontal component of the turning angle, and φ is the vertical component.

Three angles were calculated to examine average turning angle (Fig. 1): (1) α is the turning angle in three-dimensional space between consecutive runs or straight sections; (2) θ is the turning angle in the horizontal ($X$–$Y$) plane between consecutive runs; and (3) φ is the angle in the vertical ($X$–$Z$) plane between runs. Vector analysis, carried out by a computer program written in the C computer language, allowed determination of the angular change between successive vectors or runs. We determined that the larvae alter their trajectory after swimming a distance of approximately two to three body lengths, or about the distance from the centre to the edge of the video monitor. Therefore, we set run length at two body lengths. For α, the angle was unsigned; for θ and φ, a positive value indicated a turn to the left or up, and a negative value indicated a turn to the right or down. The distribution of turning angles of paths recorded here was symmetrical about zero, but had peaks for left and right turns away from zero. Accordingly, the absolute values of θ and φ were taken before further analysis. The mean and standard deviation of a series of turning angles from a single path were calculated using circular statistics (Zar 1984).

Because of difficulties associated with path analysis using conventional means of analysis (see Discussion), we used an alternative method for comparing three-dimensional swimming paths of animals: fractal geometry. Fractal analysis can be used to generate the fractal dimension ($D_f$) of a swimming path, a term that describes the effective dimension of a shape and, therefore, relative complexity (Mandlebrot 1983). A benefit of using fractal dimension is that it provides a single value to describe the shape of a path. Analysis of turning angle data contributes to an understanding of how path complexity is generated by the fish.

We calculated fractal dimension using the compass or dividers method (Peitgen & Saupe 1988; Sugihara & May 1990). The basis for this calculation is a comparison of the length of a path measured in terms of the steps of a given divider width, or step length, over a range of step lengths. Fractal dimension ($D_f$) is related to the rate of decline in number of steps with increasing step length via equation (1)

$$L(\delta) = k\delta^{1-D_f} \quad (1)$$

where δ is step length, $L(\delta)$ is number of steps, and $k$ is a constant (Mandlebrot 1983; Sugihara & May 1990). $L(\delta)$ versus δ is plotted as a log/log plot (Fig. 2), and $D_f$ is calculated as 1 minus the slope of the resulting line. In three-dimensional space, $L(\delta)$ declines with increasing δ, the slope falls between 0 and −2. Therefore, while the topographical dimension ($D_t$) of a swimming path is 3, the fractal dimension of that path can range from 1–3 (Meakin 1986; Sugihara & May 1990).

In terms of search behaviour, lower values of $D_f$ correspond to smoother, more straight paths. Higher $D_f$ values indicate increasing degrees of complexity of the path (Jander 1982; Sugihara & May 1990).

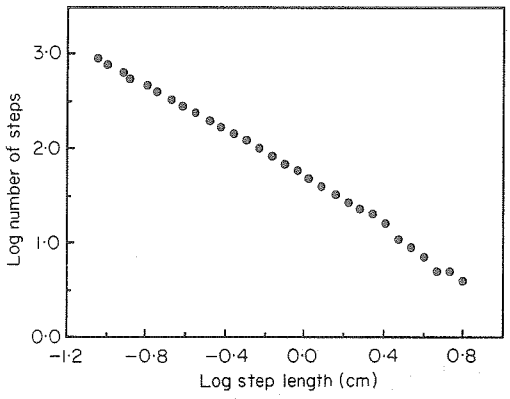


**Figure 2.** Log/log plot of the number of steps versus the step length ($\delta$) used in the calculation of fractal dimension ($D_f$) of one swimming path of an *A. perideraion* larva. The regression line is $Y = -1{\cdot}264X + 1{\cdot}673$; $r^2 = 0{\cdot}995$. $D_f = 1 - \text{slope} = 2{\cdot}264$.

For a particular $D_f$ to be considered valid, it must produce a highly linear regression ($r^2 \geq 0{\cdot}99$) over a range of step lengths greater than one order of magnitude (Fig. 2). The algorithm used to calculate fractal dimension was a three-dimensional version of that described by Rapaport (1985).

### Modelling of Swimming Paths

To investigate the effectiveness of different search patterns, we constructed a model to recreate the foraging movements of fish larvae. We combined modelled paths with the reaction distance of a foraging larva to permit determination of the prey encounter rates for larvae searching with different path shapes. We selected a reaction distance (the maximum distance at which a larva can detect its prey) of one body length, similar to the reaction distance of other models of fish larvae search patterns (Dabrowski et al. 1989). Hunter (1981) reported that one body length is near the maximum reaction distance of fish larvae, particularly for larvae with well-developed visual systems such as clownfish. By using the artificial path to direct the motion of the CritterSpy, we could videotape the microenvironment encountered by a modelled fish larva swimming along the path. As the model generated a path that was used to move the view of the CritterSpy's two cameras within the filming vessel, we could count the number of prey items passing within one reaction distance from the centre of the camera view. Encounter rate was calculated as number of prey divided by the temporal duration of the path.

To generate a path, we programmed the model with mean and standard deviation values of $\theta$ and $\varphi$ taken from observed swimming paths. As before, a run-length of two body lengths was chosen for the movement between turns. An artificial path was generated by having the computer move the distance of one run-length, turn relative to its current orientation according to a pair of model-generated turning angles ($\theta_x$ and $\varphi_x$), and then move one run-length in the new direction. The model would then direct the CritterSpy to turn according to a pair of angles ($\theta_{x+1}$ and $\varphi_{x+1}$) and move one run-length in this new direction. This process was repeated until the model ran into a wall, the bottom, or the surface of the water in the filming vessel; later analysis of the artificial search paths was stopped when each path reached a point 0·5 cm from one of these barriers.

The calculation of a turning angle, $\theta$, from a normal distribution described by a mean, $\bar{x}$, and standard deviation, $s$, involves a two-step process. First an intermediate coefficient, $w$, was found using the following equation

$$w = [\sqrt{(-2 \log u)}]\,[\cos(2\pi v)] \qquad (2)$$

where $u$ and $v$ are defined as random numbers from 0 to 1 (Craig 1988). The actual turning angle was then calculated as

$$\theta = (r\,\bar{x}) + (s\,w) \qquad (3)$$

where $r$ is randomly assigned a value of either $+1$ or $-1$ and thereby determines whether a turn is to the left or right (Craig 1988). The vertical turning angle, $\varphi$, was calculated in a similar manner.

We determined encounter rate for each of four different path specifications at three densities of food. We chose the four real paths that were modelled because: (1) they had well spaced $D_f$-values, and (2) their $D_f$-values fell close to the regression line of $D_f$ versus angle $\alpha$ (see Results). We separately programmed the mean and standard deviation of $\theta$ and $\varphi$ from each of the four real paths into the above model to generate modelled paths.

## RESULTS

*Amphiprion perideraion* larvae begin active feeding on the third day after hatching. We calculated the daily feeding rate in strikes per hour by counting the total number of feeding strikes and dividing by the duration of all swimming paths on one particular day. While on day 2 the feeding rate was 1·6

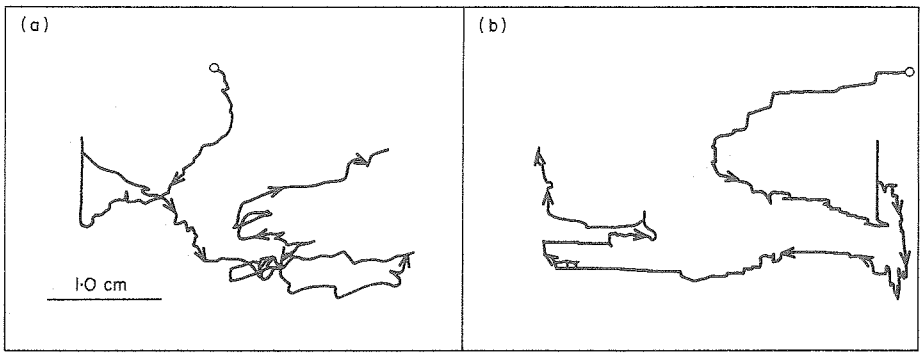


**Figure 3.** Two plots of a single swimming path in three-dimensional space of *A. perideraion* larvae at 3 days after hatching. For each plot, $Z$ is the vertical axis, (a) $X$ is the horizontal axis, and (b) $Y$ is the horizontal axis. Each drawing corresponds to one camera view. The path begins at the circle; arrows mark fish position and direction of movement at 10-s intervals. For this path, total path duration is 92·3 s, $D_f = 2{\cdot}264$ and NGDR = 0·159.

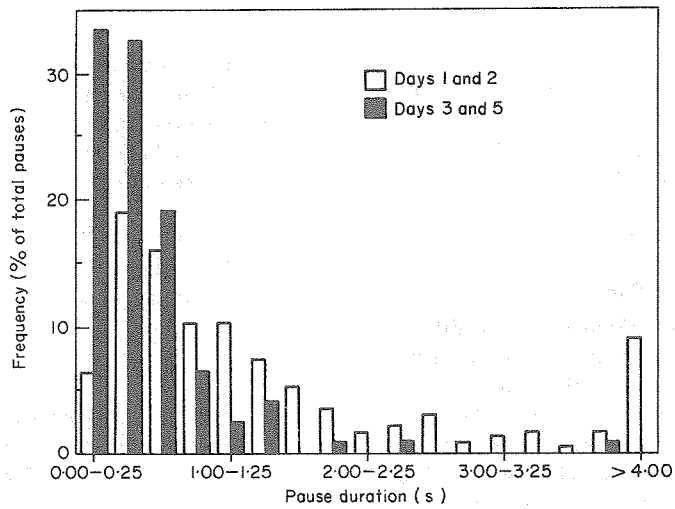


**Figure 4.** Frequency of pause duration during swimming by *A. perideraion* larvae. Data were combined for days 1 and 2 after hatching (before onset of feeding) and for days 3 and 5 (after onset of feeding).

strikes/h, by day 3 this rate had increased to 65·6 strikes/h. The increase in feeding behaviour was reflected in the growth patterns of the larvae. At hatching, pink clownfish had a mean ($\pm$SD) length of 4·22$\pm$0·12 mm ($N$=7). At day 3 when the larvae commenced feeding, mean length was 4·08$\pm$0·13 mm ($N$=7). By day 7, mean length had increased to 4·63$\pm$0·21 mm ($N$=3).

## Swimming Behaviour

When foraging for zooplankton food such as rotifers, *A. perideraion* larvae moved about actively in all three dimensions in highly variable and irregular paths (Fig. 3). Particularly when newly hatched, the fish swam in an erratic manner in bursts of 1–3 s, similar to other newly hatched fish larvae (Wyatt 1972). Between bursts, they paused and sank (Fig. 4). On day 2 they continued the pattern of burst and pause swimming, but no longer sank between bursts. By day 5 they swam continuously, generally pausing only to position themselves in front of prey items. At this point, the larvae sculled their pectoral fins to adjust position. Clownfish larvae foraging can be termed 'cruise' predation, because they are in constant motion while searching for prey. This is in contrast to fish larvae such as golden shiner, *Notemigonus crysoleucas*, which use pause-travel search (Browman & O'Brien 1992). The increase in swimming activity at the onset of feeding was

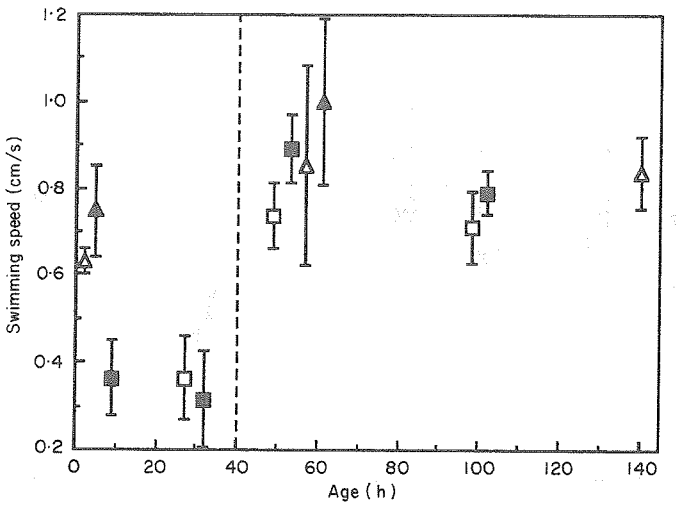


**Figure 5.** Swimming speed of *A. perideraion* larvae plotted as a function of the age of the larvae. Mean (±SD) data are from the swimming paths of the first batch of larvae at low (□) and high (■) food densities and the second batch at low (△) and high (▲) food densities. The broken line marks the onset of active feeding by the larvae.

similar to the behaviour of other fish larvae at first feeding (Hunter 1972; Kiorboe et al. 1985).

Initially swimming speeds of newly hatched fish larvae were relatively high. However, mean swimming speeds were considerably lower 8–10 h after hatching, and remained low late in the first day after hatching and during the second day (Fig. 5). After the initiation of feeding, swimming speed increased again. There was a significant relationship between age and swimming speed at both high- and low-food densities (ANOVA: low density, $F=11{\cdot}4$, $df=4, 200$, $P<0{\cdot}001$; high density, $F=29{\cdot}0$, $df=3, 28$, $P<0{\cdot}001$). Swimming speed was also related to density of food, being higher when food was more abundant (Fig. 5). Paired *t*-tests at each age where paired data was available (days 1, 2, 3 and 5) showed a significant increase in speed for days 3 and 5 of the first batch of larvae (day 3: $t=4{\cdot}50$, $P<0{\cdot}025$, $N=7$; for day 5: $t=2{\cdot}18$, $P<0{\cdot}05$, $N=5$). Significant increases in swimming speed at high food densities were observed only after the initiation of active feeding.

## Search Patterns

The NGDR of swimming paths of *A. perideraion* larvae showed no significant trends with increasing age or with changing prey density, and was found to be an ineffectual statistic because of the high levels of variance, or 'noise', observed throughout this study (Fig. 6). Paired *t*-tests for each date found no significant differences between low- and high-density swimming paths with respect to NGDR (in all cases $P>0{\cdot}25$). One-way ANOVAs for both low and high density found no relationship between age and NGDR ($P>0{\cdot}25$).

## Fractal Analysis

During the first 2 days after hatching, *A. perideraion* larvae had relatively highly convoluted and highly variable swimming paths, as indicated by the fractal dimension, $D_f$, of those paths. Once the fish began actively feeding during the third day, $D_f$ was generally much lower, indicating an overall trend to more linear and less complex paths (Fig. 6). Age had a significant effect on $D_f$ at low density (ANOVA: $F=4{\cdot}80$, $df=4, 19$, $P<0{\cdot}01$), but at high density, the relationship of age to $D_f$ was less clear ($F=2{\cdot}40$, $df=3, 27$, $P<0{\cdot}10$). There was a significant relationship of age with the variance of $D_f$ at low density as well (Barlett's test of the homogeneity of variance: $B_c=16{\cdot}45$, $df=4$, $P<0{\cdot}005$, $N=27$); there was less variance in $D_f$ among the older larvae. This same relationship was not found to be significant for larval swimming tracks in high prey density ($B_c=5{\cdot}18$, $df=3$, $P>0{\cdot}25$, $N=32$).

After the onset of active feeding, *A. perideraion* began to use different search patterns in low versus high density. In low density, $D_f$ was the lowest and

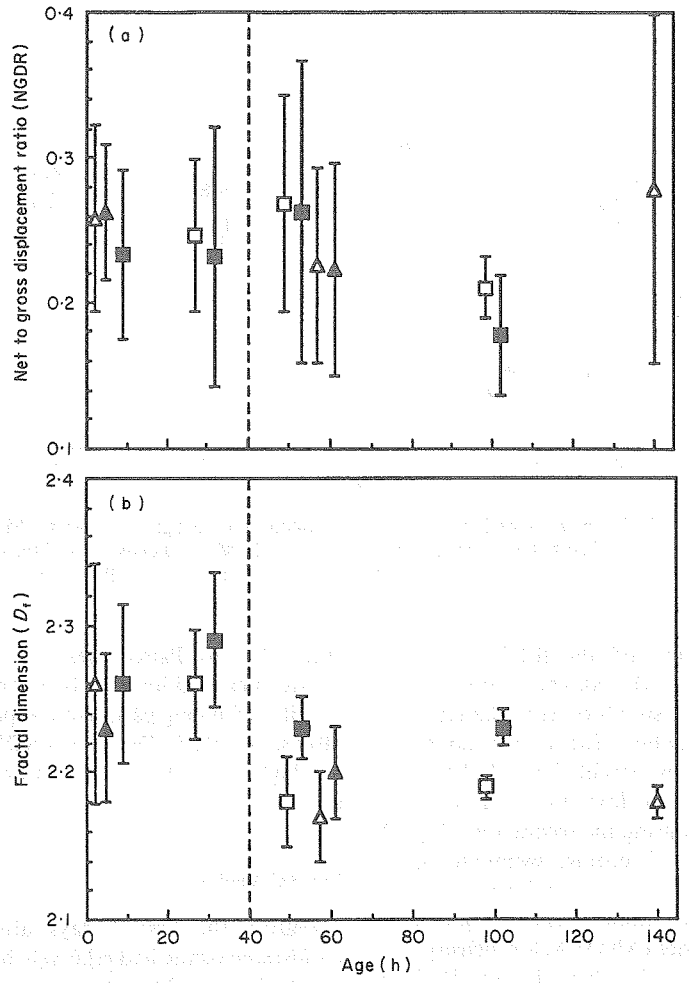


**Figure 6.** (a) Net to gross displacement ratio and (b) fractal dimension ($D_f$) of swimming paths of *A. perideraion* larvae as a function of age. Mean (±SD) data are from the swimming paths of the first batch of larvae at low (□) and high (■) food densities and the second batch at low (△) and high (▲) food densities. The broken lines mark the onset of active feeding by the larvae.

the fish swam in relatively straight paths. The complexity of swimming paths increased at the higher prey density (Fig. 6). There was a significant difference between the $D_f$ of swimming paths of fish larvae in low versus high prey density for days 3 and 5 (Paired $t$-test: day 3, $t=2{\cdot}376$, $P<0{\cdot}05$, $N=4$; day 5, $t=6{\cdot}426$, $P<0{\cdot}005$, $N=4$). A shift in the $D_f$ of search paths from 2·19 at low density to 2·23 at high density, such as that observed for day 5 larvae, did make a difference in the shape of swimming paths (Fig. 7). Over this range, the paths became progressively more complex and the fish searched a more restricted area, as is apparent in a visual survey of the plots of the paths.

The mechanism by which *A. perideraion* alter the $D_f$ of their search patterns may relate to both the mean and the variance of the turning angles within the search paths (Fig. 8). $D_f$ increased with both increasing mean α and increasing standard deviation about the mean α. The regression lines were significant for plots of $D_f$ versus mean α (ANOVA testing: $F=27{\cdot}2$, $df=1, 79$, $P<0{\cdot}01$) and circular standard deviation ($F=33{\cdot}8$, $df=1, 79$, $P<0{\cdot}01$). The swimming paths of larvae foraging in high prey density had higher values of mean α and variance

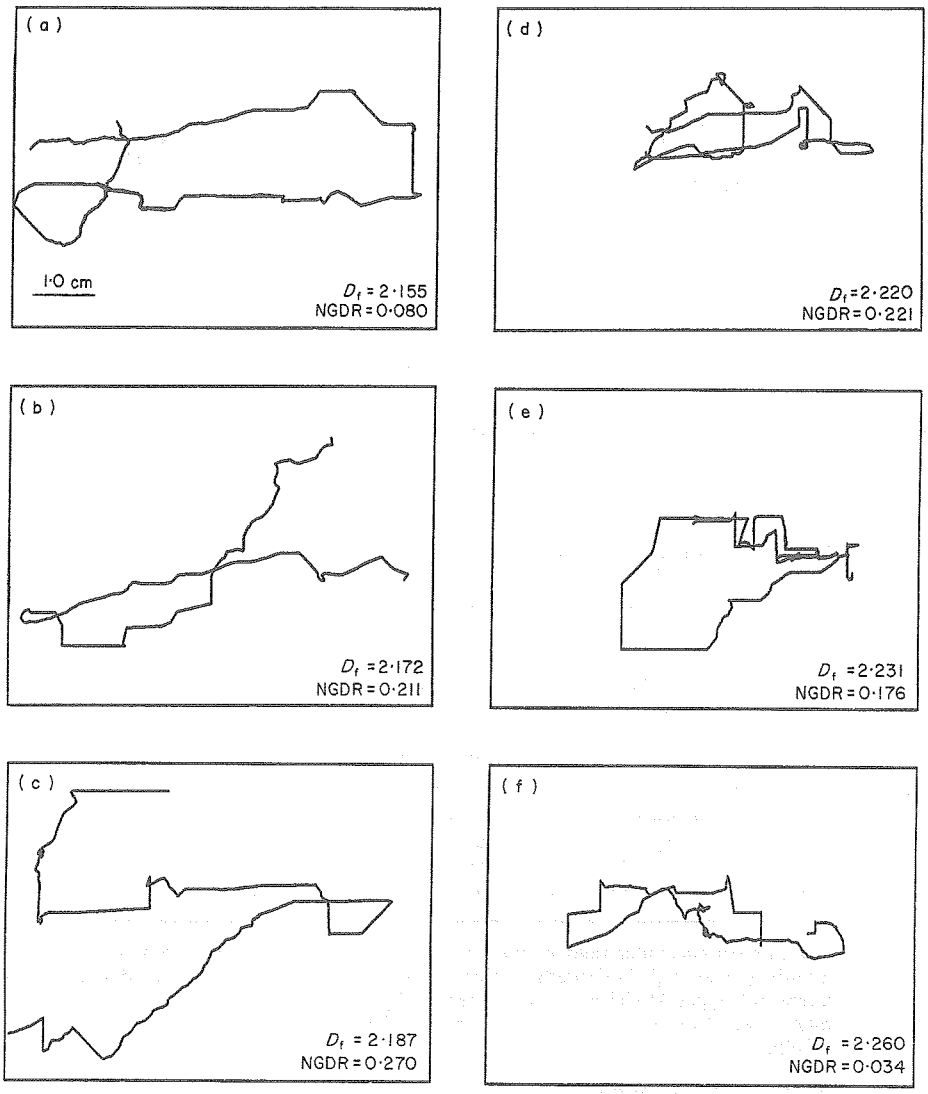


**Figure 7.** Projections onto the $X$–$Z$ plane of the three-dimensional swimming paths of *A. perideraion* larvae at 5 days after hatching. These plots (a–f) were chosen to represent paths at each fractal dimension ($D_f$). While $D_f$ increases, net to gross displacement ratio, NGDR, does not have a clear trend.

about the mean. Therefore, they had higher values of $D_f$.

## Modelled Search Paths

From the results of the experiment modelling different search paths of fish larvae in several food densities, it was evident that the complexity of swimming paths did affect the encounter rate of fish larvae. Encounter rate decreased as complexity (i.e. $D_f$) increased (Table I). Particularly at low prey densities, a modelled fish encounters less food when swimming a complex path. Since a fish that swims a highly convoluted path will tend to search areas repeatedly, encounter rate may drop because the fish spends too much time searching areas redundantly. At higher prey densities, this relationship is not as strong. During the modelling experiments, at middle and high densities, a significant proportion of the rotifers in the filming vessel were collected at

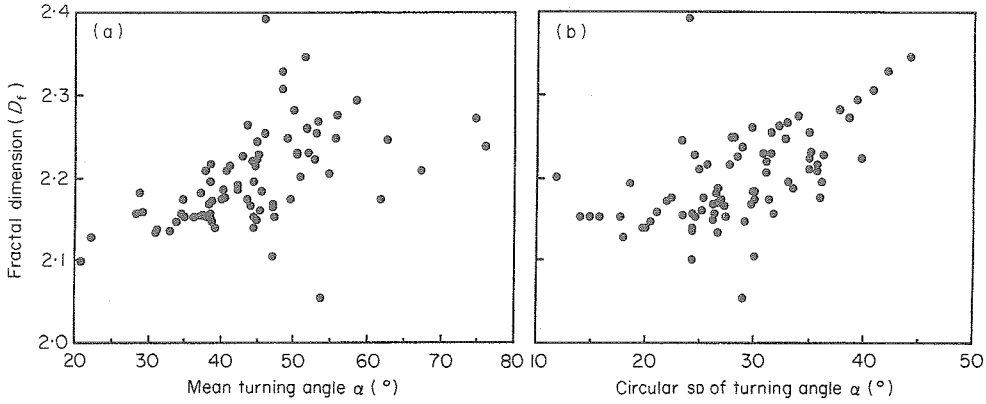


**Figure 8.** Scatterplots of fractal dimension ($D_f$), versus (a) mean turning angle α: $r^2=0{\cdot}261$, $Y=0{\cdot}170\,X+2{\cdot}067$ and (b) circular standard deviation of α: $r^2=0{\cdot}305$, $Y=0{\cdot}276X+2{\cdot}061$ for single swimming paths of *A. perideraion* larvae.

**Table I.** Modelled prey encounter rates compared with increasing complexity of swimming path at several prey densities

| | Prey density | | | | | |
|---|---|---|---|---|---|---|
| | Low (20/litre) | | Medium (100/litre) | | High (1000/litre) | |
| $D_f$ | Encounter rate | *N* | Encounter rate | *N* | Encounter rate | *N* |
| 2·099* | 14·86±5·13 | 8 | 33·49±7·26 | 12 | 54·63±7·83 | 10 |
| 2·187† | 11·33±2·70 | 11 | 28·63±8·55 | 8 | 48·40±8·47 | 9 |
| 2·231‡ | 10·64±3·12 | 8 | 20·83±3·11 | 8 | 42·53±6·02 | 8 |
| 2·315§ | 5·78±1·03 | 8 | 16·37±3·10 | 7 | 36·80±7·26 | 8 |

Mean (±SD) encounter rates in rotifers per minute were determined from video-recordings made with the CritterSpy by programming camera movements according to several path types. Modelled path types, denoted by $D_f$, used mean (±SD) turning angle values taken from real paths as stated in the following notes (see Fig. 3 for angle definitions).
*$\theta=23{\cdot}7\pm25{\cdot}4$, $\varphi=12{\cdot}8\pm23{\cdot}8$.
†$\theta=34{\cdot}1\pm37{\cdot}1$, $\varphi=26{\cdot}9\pm36{\cdot}3$.
‡$\theta=45{\cdot}4\pm36{\cdot}6$, $\varphi=44{\cdot}2\pm34{\cdot}5$.
§$\theta=70{\cdot}5\pm43{\cdot}7$, $\varphi=65{\cdot}9\pm52{\cdot}3$.

the surface, so that the actual prey density was somewhat lower than the nominal stocking density. At high prey densities, though, the trend of lower encounter rate with increasing search path complexity was still apparent.

## DISCUSSION

*Amphiprion perideraion* larvae forage in a manner that has both similarities to and differences from conventional foraging paradigms. Like other foragers, clownfish larvae respond in a non-random way to varying densities of food. When food is in high abundance they use more complex and convoluted swimming modes. The geometry of their search patterns affects both the encounter rate and the efficiency of the exploitation of patchy resources. Unlike other foraging animals, actively feeding *A. perideraion* larvae move at higher velocities when they encounter high prey densities,-possibly due to hydrodynamic constraints relating to their small size (see below).

### Search Behaviour

Once they began actively feeding on rotifers around the third day after hatching, *A. perideraion* exhibited different behavioural modes when food was in low abundance as opposed to when food was in high abundance. The effect of these two modes is (1) to maximize encounter rate when food is in low abundance (i.e. to find a patch) and (2) to maintain position within a small area when encountering food in high abundance (i.e. to stay within a patch). These modes are based on differences in turning rate such that at low food density, the fish make shallow turns and have more linear paths, while at high density, the fish make wider angled turns and have highly complex paths. This agrees in principle with results for many other animals, including fish larvae (Rosenthal & Hempel 1970; Hunter & Thomas 1974; Munk & Kiorboe 1985).

Fish larvae face a trade-off of decreasing encounter rates as a price for maintaining position within a patch. Results of the modelling experiment reported here indicate that in a homogeneous environment, a smooth, linear path generates the highest relative encounter rate. These results agree with a similar modelling experiment using three-spined sticklebacks, *Gasterosteus aculeatus* (Beukema 1968). When foraging in an area of high food density, *A. perideraion* larvae use a complex swimming path. Since foraging with this path type does not generate the maximum encounter rate, these fish may alter their swimming behaviour in response to other factors.

If food is distributed in patches, searching with complex swimming paths will result in a higher rate of food intake over time because the larvae will spend more time in each patch. Redundancy in search movements, the result of searching with a complex path, increases effectiveness of search for patchy or lumped prey (Winkelman & Vinyard 1991). Krebs (1973) points out that a complex, area-restricted search is the best mechanism for searching in a patchy environment. This holds true for fish larvae foraging on rotifers, where there is (1) a relatively fast-moving predator actively searching for a small, slow-moving prey and (2) the predator has a reaction distance on the same scale as its body size. If the prey speed exceeds predator speed, the prey's path is relatively complex and/or the prey are difficult to locate, a predator will maximize prey encounter rate by using a more linear path (Krebs 1973).

### Swimming Behaviour

In general, many animals slow down their rate of movement when they encounter high food abundance, this includes fish larvae (Rosenthal & Hempel 1970; Wyatt 1972; Hunter & Thomas 1974; Munk & Kiorboe 1985). Slowing down is apparently a mechanism used by many animals to stay within a patch of high food density. *Amphiprion perideraion* larvae do not behave in this manner; they increase swimming speed when they encounter a high abundance of food.

Clownfish larvae may increase swimming velocity in response to high prey densities because of constraints imposed by the viscosity of the water in which they live. Because clownfish larvae are relatively small, they swim under different hydrodynamic conditions from adult fish. As size and swimming speed decrease, so does the relative influence of inertia, while the effect of viscosity increases. This relationship is expressed by the dimensionless Reynolds number (*Re*) which is the ratio of inertial to viscous forces acting on an object (Vogel 1981). The lower the Reynolds number, the greater the effect of viscosity.

Clownfish larvae make turns by bending their body and gliding through an arc. They rely upon their momentum to carry them through a turn; viscous drag, however, tends to stop them quickly when they coast, as has been suggested for zebra danio larvae, *Danio rerio* (Fuiman & Webb 1988). To make wider-angled turns larvae must coast further, and must therefore have a higher initial speed to overcome the consequences of viscous drag.

Fuiman & Webb (1988) reported a relationship between turning angle and Reynolds number in zebra danios, *D. rerio*. When swimming slowly ($Re < 23$) *D. rerio* larvae turn with only shallow angles. With age and increasing body length and swimming speed ($23 < Re < 75$) danio larvae turn with either shallow turns, averaging 3°, or with very wide turns, averaging 105°. The fish consistently move faster before making a wide-angle turn (Fuiman & Webb 1988). The swimming of *D. rerio* larvae falls into a transitional range of Reynolds number ($< 10$ to $> 30$), where the viscous drag exerted upon an object drops rapidly with increasing Reynolds number. As viscous drag drops, the relative importance of inertia increases, making coasting possible (Weihs 1979; Osse 1990).

*Amphiprion perideraion* larvae may speed up in response to high food density simply to facilitate

**Table II.** Length, swimming speed, water temperature and approximate Reynolds number (*Re*) of four species of first feeding fish larvae

| Species* | Length (mm) | Speed (mm/s) | Temperature (°C) | *Re* |
|---|---|---|---|---|
| *Amphiprion perideraion* | 4·1 | 9·0 | 24 | 38 |
| *Clupea harengus* | 11·0 | 10·0 | 10 | 81 |
| *Engraulis mordax* | 2·9 | 1·5 | 19 | 4 |
| *Scomber japonicus* | 3·6 | 5·0 | 19 | 16 |

*Source in order presented: this study; Rosenthal & Hempel (1970); Hunter & Thomas (1974); Hunter & Kimbrell (1980).

turning through wide angles. These wider turns allow the larvae to swim in a more convoluted path and, thereby, to stay within a patch of food. The Reynolds number of an *A. perideraion* larva at first feeding is about 38 (Table II). This falls within the intermediate zone, where increasing speed relates to wider turns, described by Fuiman & Webb (1988).

The question arises as to why other fish larvae slow down their swimming speed when they encounter high food abundance. Herring larvae, *Clupea harengus*, swim with a higher Reynolds number, above the intermediate zone, and therefore may not be constrained by viscous forces. Although anchovy larvae, *Engraulis mordax*, move at a very low Reynolds number (Table II), their swimming speeds are based on an average over several minutes (Hunter & Thomas 1974) and since they swim with a burst and glide pattern (Hunter 1972), their Reynolds number during the bursts of swimming may actually be much higher, falling within the intermediate zone. First feeding *E. mordax* are capable of burst speeds greater than 40 mm/s (Hunter 1972), which would give them a Reynolds number of over 100, well into the intermediate zone. Similarly, given that on day 2, when *A. perideraion* larvae swim at slow speeds but in highly complex paths, these fish may be able to make wide turns because of high Reynolds number values achieved during rapid bursts of swimming.

### Analysis of Search Behaviour in Aquatic Systems

In this paper we document the first analysis of the swimming behaviour of fish larvae with fractal geometry. The benefit of fractal geometry, particularly in three-dimensional systems, is that it gives a value, $D_f$, to describe the shape of swimming patterns. Compared with other, more conventional methods of analysis, fractal geometry has far less variability in its results (Dicke & Burrough 1988). To describe the swimming paths of free-swimming zooplankters, a term such as NGDR is susceptible to chance because of the nature of swimming patterns in the plankton. Small aquatic animals tend to swim with paths that cross over on themselves, even if the path is highly linear overall. Thus, one can calculate low NGDR values for paths that are generally linear, or relatively high NGDR values for highly convoluted patterns, depending on the position of the beginning and end of the path in question (Fig. 7). This has led to a greater degree of ambiguity in the results (e.g. Wong et al. 1985).

Another advantage of fractal analysis is that it provides a single term for a single swimming path. This facilitates comparison of the shape of different paths, particularly between groups of paths that need to be compared based on their mean and variance. Analysis of turning angle compliments fractal geometry, because it gives a basis for understanding how a particular $D_f$ was generated. Comparisons of search behaviour of different groups of paths based on turning angles become more difficult, though, because of the necessity of using both the mean turning angle of each path and the variance around that mean (Fig. 8). Furthermore, turning angles are generally calculated as the angle between consecutive short runs that build the overall search path. Because the length of the 'run' is picked by the researcher, its accuracy and its importance to the animal are questionable.

The CritterSpy is an improvement over previous research techniques for studying the swimming paths of fish larvae. Other studies have often been limited to either qualitative description of swimming behaviour (e.g. Munk & Kiorboe 1985) or to mathematical analysis of movement in only two

dimensions (e.g. Hunter & Thomas 1974). For larvae that have a significant amount of their movement directed vertically, such as *A. perideraion*, data of position in all three dimensions is indispensable. Skiftesvik & Huse (1987) describe a three-dimensional, computer-controlled filming apparatus used to track free-swimming fish larvae. While this apparatus has the advantage of having a much larger filming vessel (70 litres), it uses only one camera and is thereby limited in its ability to produce fully three-dimensional data. Additionally, the computer only logs the position of a fish once per second. The CritterSpy accurately details swimming paths in three dimensions at a more rapid rate (10–15 Hz).

In summary, *A. perideraion* larvae, like other animals, forage using at least two modes of search behaviour: one corresponds to ranging, the other to local search. In nature, these foraging modes may be used to locate and exploit food patches, respectively. Because conventional means of analysis failed to discriminate differences in behaviour, comparison of the non-temporal components of foraging movements (i.e. the shape of search patterns) of clownfish larvae required the use of an alternative method of analysis, fractal geometry.

Additionally, *A. perideraion* increase their rate of movement when shifting from ranging to local search, in contrast to other animals. Clownfish larvae apparently are under special constraints as a result of their small size and slow swimming speed, and therefore, have a disadvantageous ratio of inertial versus viscous forces of their surrounding water, as expressed by a low Reynolds number. Because the temporal component of foraging movements (i.e. swimming speed) of a foraging zooplankter is constrained by hydrodynamic forces, models of search behaviour that predict optimal search speeds (e.g. Dabrowski et al. 1988) need to be tempered by information regarding the physical forces acting upon a foraging organism.

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